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The exotic invasive plant *Vincetoxicum rossicum* is a strong competitor even outside its current realized climatic temperature range

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Abstract

Dog-strangling vine (*Vincetoxicum rossicum*) is an exotic plant originating from Central and Eastern Europe that is becoming increasingly invasive in southern Ontario, Canada. Once established, it successfully displaces local native plant species but mechanisms behind this plant's high competitive ability are not fully understood. It is unknown whether cooler temperatures will limit the range expansion of *V. rossicum*, which has demonstrated high tolerance for other environmental variables such as light and soil moisture. Furthermore, if *V. rossicum* can establish outside its current climatic limit it is unknown whether competition with native species can significantly contribute to reduce fitness and slow down invasion. We conducted an experiment to test the potential of *V. rossicum* to spread into northern areas of Ontario using a set of growth chambers to simulate southern and northern Ontario climatic temperature regimes. We also tested plant-plant competition by growing *V. rossicum* in pots with a highly abundant native species, *Solidago canadensis*, and comparing growth responses to plants grown alone. We found that the fitness of *V. rossicum* was not affected by the cooler climate despite a delay in reproductive phenology. Growing *V. rossicum* with *S. canadensis* caused a significant reduction in seedpod biomass of *V. rossicum*. However, we did not detect a temperature x competition interaction in spite of evidence for adaptation of *S. canadensis* to cooler temperature conditions. We conclude that the spread of *V. rossicum* north within the tested range is unlikely to be limited by climatic temperature but competition with an abundant native species may contribute to slow it down.

Keywords

Dog-Strangling Vine, *Vincetoxicum rossicum*, invasive species, invasion ecology, competition, phenotypic plasticity, climatic temperature range, spread, reproductive phenology

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Introduction

Dog-strangling vine (*Vincetoxicum rossicum* (Kleopow) Barbar.*; syn. Cynanchum rossicum* (Kleopow) Borhidi) is an alien invasive plant species from the Ukraine and southwestern Russia that has established in the north-eastern United States and southern Ontario. *Vincetoxicum rossicum* was first found in Toronto in 1889 (Smith et al. 2006). It is a perennial self-pollinating vine that produces pods filled with comose seeds that are wind-dispersed. *Vincetoxicum rossicum* effectively competes for light by forming large and dense stands that climb over other plants. This life-strategy results in suppression of native plant productivity and diversity (DiTommaso et al. 2005). *Vincetoxicum rossicum* has been found growing successfully in both disturbed and undisturbed areas, in open fields, forest edges and understories, parks, road edges and railway embankments. The species produces a dense and fibrous root system and demonstrates wide environmental tolerance to variations in light intensity and soil moisture (DiTommaso et al. 2005; Douglass et al. 2009).

Currently, the distribution range of *V. rossicum* in North America has temperature and precipitation limits similar to those found in its native range (Kricsfalusy and Miller 2010). This climatic distribution pattern is consistent with what occurs for many exotic invasive terrestrial plants. A recent study on Holarctic invasive plants indicates that their new invaded range matches their native realized climatic niche, and that most species do not tend to invade beyond that range (Petitpierre et al. 2012). However, given the high degree of environmental tolerance shown by *V. rossicum*, which factor(s) may be preventing its northern range expansion? Is it possible that nothing is limiting its expansion (i.e., propagules have simply not reached the north) or specific factors (e.g., climatic, edaphic, environmental disturbance, biotic interactions) are preventing establishment? Considering the large number of seeds produced and their anemochory, it is unlikely that expansion is being limited by low propagule pressure.

It is unknown the extent to which climate serves as a barrier for further spread in the introduced range. Areas of central/northern Ontario that have, on average, slightly cooler temperatures than those in the vine's current range might be at risk of invasion by this plant. As such, determining the phenology and fitness of *V. rossicum* under those conditions is required for risk assessment and to potentially adjust management practices.

Plant phenology can be influenced by abiotic and biotic factors (Pau et al. 2011) and provides invasive plants with a competitive advantage over native plants. For instance, accurate timing of budburst can allow invasive plants to outcompete native species for light and successfully timed reproductive phenology ensures higher levels of fitness (Wolkovich and Cleland 2011; Godoy et al. 2008). Analyses of long-term phenological responses of native and exotic plant species to climate change have indicated that exotic invasive species are better able than natives at adjusting their flowering time (Willis et al. 2010).

Field studies on plant phenology have indicated that temperature cues have a large influence on flowering in many species (Pau et al. 2011; Fitter et al. 1995; Vasek and Sauer 1971). If a potentially invasive plant cannot adjust its phenology to its new climate,

its chances of establishing a successful population may be drastically reduced. Therefore, environmental tolerance, phenotypic plasticity and/or adaptive evolution may be crucial factors for invader success. Since invasion by *V. rossicum* is currently restricted to areas of North America with a climate similar to that found in its native range, its potential to spread throughout the introduced range is unknown. Nevertheless, flowering is found to occur later in Ontario than in populations from the United States, indicating a potential climate-influenced phenological gradient (Douglass et al. 2009; DiTommaso et al. 2005). Species-distribution models have indicated that the northern limits of a plant's range may be strongly influenced by its inability to set mature seeds (Morin et al. 2007). Therefore, *V. rossicum* may be limited in its capacity to spread into northern climates simply because it may not be able to complete its life-cycle.

On the biotic side, interspecific competition may be a limiting factor in species distribution (Keddy et al. 1998). Therefore, understanding competitive interactions between invasive and native species is important in risk assessment and can result in novel or improved management and restoration approaches (Firn et al. 2010). In its current North American range, *V. rossicum* is able to form what are essentially monocultures (DiTommaso et al. 2005), which would suggest that it is an excellent competitor against native species. Competitive ability has been tested in regard to *V. rossicum* polyembryony (Blanchard et al. 2010) and potential allelopathy (Douglass et al. 2011); both studies incorporated native species that co-occur with *V. rossicum* and ran from periods ranging 2–15 weeks in length under static growing conditions. However, there are no data on whether *V. rossicum* responds negatively to a highly abundant native species outside its current climatic range.

The purpose of this study was two-fold. First, we investigated whether *V. rossicum* could grow under the cooler climate of northern Ontario, and whether any observed phenological changes could represent a barrier to the successful establishment of this invasive plant. Secondly, we tested the response of *V. rossicum* to the presence of a perennial abundant native plant (i.e., Canada goldenrod - *Solidago canadensis* L. var. *canadensis*) whose center distribution range is northern Ontario, and how the competitive interaction was affected by the shift in temperature. We selected *S. canadensis* as our competing species because it co-occurs with *V. rossicum* (Kricsfalusy and Miller 2010; Averill et al. 2008; Cappuccino 2004), and is prominent in both climate regimes simulated in our study. However, it is unknown if *V. rossicum* can invade *S. canadensis* populations in southern Ontario or the United States or vice-versa. *S. canadensis* is considered an invasive species in Europe and Asia (Abhilasha et al. 2008), suggesting that it may have strong competitive abilities in its native range. We hypothesised that this native plant might possess the competitive ability to withstand invasion by *V. rossicum* and produce a detrimental effect on its growth and fitness. While this ability may be out-performed by *V. rossicum* under the invasive plant's climatic range, it may exceed that of *V. rossicum* when allowed to grow under a climate that is established as suitable for *S. canadensis* but may prove challenging to *V. rossicum.* If this is the case, seeding with *S. canadensis* in areas invaded by *V. rossicum* may serve as an effective and environmentally friendly tool for management purposes on invaded sites.

Materials and methods

Dog-strangling vine (*Vincetoxicum rossicum* (Kleopow) Barbar.) root crowns were collected in Rouge Park, Toronto, ON (43.80526°N, 79.13594°W) in early May, 2011, before the onset of the growing season. The substrate used in the experiment consisted of soil collected from an un-invaded site adjacent to one invaded by *V. rossicum*. Root crowns were planted in one side of 10 L pots that were divided in half by a nylon mesh (30 μm opening) (Sefar Nitex 03-30/18, Heiden, Switzerland), which allows water and microbes, including fungal hyphae, to cross but prevents roots. The use of this nylon mesh still allows plants to compete for water and nutrients through diffusion, mass flow and mycorrhizal networks while preventing the roots from intertwining. The pots were filled with a 13 cm layer of a 2:1 mixture of Turface (a montmorillonite clay, Turface Athletics MVP, Profile Products LLC, Buffalo Grove, IL, USA) and non-calcareous granitic sand (Hutcheson Sand and Mixes, Huntsville, ON) followed by a 10 cm layer of 1.2 kg of field soil, and an additional 3 cm of the Turface:sand mixture.

The experiment consisted of a completely randomized block design with two crossed factors; 'plant competition' and 'temperature'. Specifically, for 'plant competition' *V. rossicum* plants were either planted alone (control) or with a Canada Goldenrod *(Solidago canadensis* L. var. *Canadensis*; seeds were collected in the north eastern United States by Ontario Seed Company, Waterloo, ON, Canada) seedling in the other half of the pot (competition group). *Solidago canadensis* seedlings were also planted alone (*S. canadensis* control). Each of these treatments comprised a total of 24 pots, which were divided evenly among six reach-in controlled environment units (Conviron, Winnipeg, MN, Canada), each representing a block; three chambers were set to Toronto (TO) growing season temperatures and three chambers set to Sault Ste. Marie (SSM) growing season temperatures for an overall total of 72 pots. To minimize any potential variability among controlled environment units all respective pots were rotated among units and re-randomized within each block every 25 days. Toronto temperatures are on average approximately 3° C warmer than SSM. We used weather records collected by Environment Canada from 1980–2010 to simulate the monthly temperature conditions throughout the growing season (Table 1). We also used these data to simulate photoperiod throughout the growing season. Since photoperiod was similar between the two locations and the main goal was to test temperature effects, it was kept the same across treatments (Table 1).

Plants were allowed to grow for five months (simulated "May" to "September"). During this time we recorded daily reproductive phenology measurements for *V. rossicum* (presence of first flower bud, first flower opening and seedpod production). Plants were watered to field capacity every second day to ensure that water deficiency was not a factor in the experiment. Since we noticed mild signs of nutrient deficiency in all plants, all pots were fertilized with Miracle-Gro 24:8:16 (The Scotts Company LLC, Mississauga, ON, Canada) (0.84 ppm P per pot) after the first month of growth. In addition all pots received a solution of 12-0-44 fertilizer (6 ppm N per pot) and

Table 1. Temperature regimes used to simulate Toronto (TO) and Sault Ste. Marie (SSM) growing seasons in the controlled environment units.

Location	Range[†]	May	June	July	August	September
		Simulated temperature (°C)[Δ]				
TO	High	20.3	25.5	28.4	27.4	23.0
	Average	14.5	19.9	22.7	21.9	17.5
	Low	8.8	14.2	17.1	16.5	12.1
SSM	High	17.9	22.8	25.5	24.8	20.3
	Average	11.4	16.2	19.2	18.9	14.8
	Low	5.0	9.7	12.9	13.0	9.4
		Simulated photoperiod (hours of light per day)[‡]				
		14h; 15h	15h	15h; 14h	14h; 13h	13h

[†] Simulated temperatures were 1.4 °C warmer than the calculated average to meet the minimum range allowed by the spell out controlled environment units (i.e., 5.0°C).

[Δ] Maximum and minimum temperatures were each maintained for 6 hours, with the remaining 12 hours set at average temperatures.

[‡] Average light intensity ranged between 350–400 μmol m^{-2} s^{-1}. When two values are given, this indicates the changing day length during that month.

slow-release 18-6-8, 70-day fertilizer (meaning that after 70 days, 80% of the nutrients would have been released into the soil; 0.72 ppm N per pot) (Nutricote, Plant Products Co., Brampton, ON, Canada) after the fourth month of growth. The use of low fertilizer concentrations and of a slow release fertilizer ensured that plants had sufficient nutrients to survive but that soil fertility was such that they had to compete for nutrients. In the final month of the experiment, plants experienced an outbreak of thrips in all chambers, and were sprayed with Nemasys nematode spray (50 million count, Becker Underwood, SK, Canada).

The commercial seed stock of *S. canadensis* was contaminated with other species of goldenrod and asters. This resulted in twelve pots (three alone and six in competition under TO temperatures and three in competition under SSM temperatures) containing the "wrong" plant species, which could not be differentiated until two months into the experiment. These pots have been removed from the competition data analysis, but have been kept for the *V. rossicum* phenology analysis.

At the end of the experimental period (as determined by simulated 'first frost date' for SSM), all plants were harvested. Roots and shoots were placed in separate bags, dried for three days at 60°C and weighed. Competitive response was calculated for both plant species according to methodology by Goldberg et al. (1999). Specifically, we calculated relative yield by dividing the total biomass of an individual plant grown with a competitor by the average total biomass for that same plant species grown alone. Competitive response was calculated by the ln of the relative yield; a negative number indicates a negative response to competition whereas a positive number indicates a positive response to competition.

Statistical analysis

We analysed plant responses to temperature on phenological data (i.e., flower budding, open flowering and Seedpod formation), total plant biomass, root : shoot ratio, and competitive response. Since pots were rotated and re-arranged randomly among controlled environment units as blocks to minimize the potential for chamber effects, block effects were tested first within each temperature group using one-way ANOVAs. If a block effect was not detected, factorial ANOVAs were carried out. When testing phenology, total biomass, and root : shoot ratio each plant species was tested individually with the factor 'plant competition' being comprised of two levels (i.e., either *S. canadensis* or *V. rossicum* alone or the response of that species in presence of the competitor). To test for competitive response the model included 'plant competition' and 'temperature' as factors. Data were Box-Cox transformed to meet the test's assumptions. All statistical analyses were carried out using Statsoft Inc. (2010).

Results

There were no significant differences in the reproductive phenology (i.e., presence of first flower bud, first flower opening and seedpod production) of *V. rossicum* grown either alone or with a competitor. In addition, we did not find a significant interaction between competition and temperature for any of these response variables. Temperature, however, had a significant effect on the reproductive phenology of *V. rossicum* (Fig. 1). Plants grown under SSM temperatures took significantly longer to produce flower buds ($F_{1,44}$ = 9.270, p = 0.00392), open flowers ($F_{1,44}$ = 11.040, p = 0.00180), and seedpod ($F_{1,44}$ = 19.778, p = 0.00006). These traits were delayed by an average of 8, 9 and 11 days, respectively, under the cooler SSM temperatures. By the end of the experimental growing season, however, all *V. rossicum* plants had produced the same biomass and number of seedpods containing mature seeds regardless of temperature treatment (Fig. 2A and C). Conversely, growing *V. rossicum* with a competitor caused significant reductions in the seedpod biomass of *V. rossicum* ($F_{1,36}$ = 42.812, p = 0.000001) and in the number of seedpods produced ($F_{1,36}$ = 30.73, p = 0.000003) (Fig. 2B and D). We did not detect a significant interaction between temperature and competition for seedpod biomass or number.

Depending on the species, total plant biomass was affected by either temperature or competition. The total biomass of *V. rossicum* was not influenced by temperature but it was significantly affected by competition ($F_{1,35}$ = 8.3459, p = 0.007), and we did not detect a competition x temperature interaction (Table 2). *Vincetoxicum rossicum* was approximately two times more competitive than *S. canadensis* ($F_{1,25}$ = 4.60392, p = 0.042) (Fig. 3). *Vincetoxicum rossicum* plants grown with *S. canadensis* were 22% smaller than plants grown alone whereas *S. canadensis*

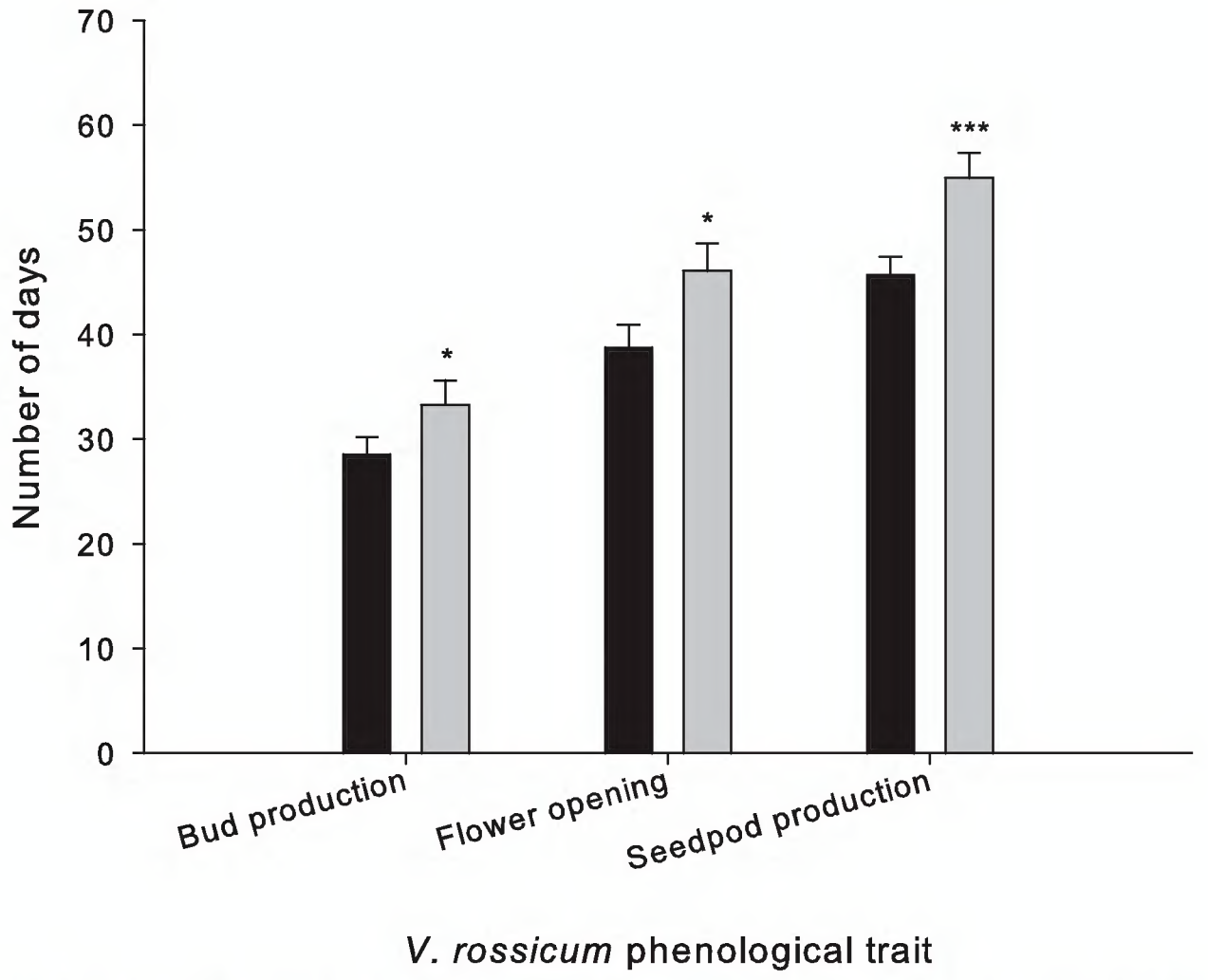

Figure 1. Number of days necessary for the production of buds, flowers and seedpods under TO (black bars) and SSM (grey bars) temperatures. Significant differences between temperature regimes for each phenological trait are indicated by * ($p<0.05$) ** ($p<0.01$) and *** ($p<0.0001$). Error bars represent the standard error of the mean (n = 24).

Table 2. Total biomass (g) and root : shoot ratio of *V. rossicum* and *S. canadensis* grown under Toronto (TO) and Sault Ste. Marie (SSM) temperature regimes and either alone or in competition with each other.

	Total biomass (g)		**Root : shoot ratio**	
	V. rossicum	***S. canadensis***	***V. rossicum***	***S. canadensis***
TO	23.56 ± 1.50	54.92 ± 4.90	2.05 ± 0.17	1.91 ± 0.18
SSM	22.75 ± 1.39	80.27 ± 8.99*	1.93 ± 0.19	2.97 ± 0.37
Alone	25.27 ± 1.39	82.46 ± 8.55	1.72 ± 0.14	2.42 ± 0.29
Competition	19.68 ± 0.86**	51.86 ± 5.23**	2.41 ± 0.20*	2.68 ± 0.42

For each species, statistically significant differences for each appropriate treatment factor are represented by * ($p<0.05$) and ** ($p<0.001$). Data are presented as mean ± standard error of the mean. (*V. rossicum,* temperature: n = 18 (TO), n = 21 (SSM); *V. rossicum,* plant species assembly: n = 24 (alone), n = 15 (competition); *S. canadensis*, temperature: n = 15 (TO), n = 21 (SSM); *S. canadensis*, plant species assembly: n = 21 (alone), n = 15 (competition)).

plants were 37% smaller when competing with *V. rossicum* ($F_{1,32}$ = 12.914, p = 0.001) (Table 2; Fig 3). Growing temperature influenced the total biomass of *S. canadensis*. Plants grown under the cooler SSM conditions were 1.5 fold larger than

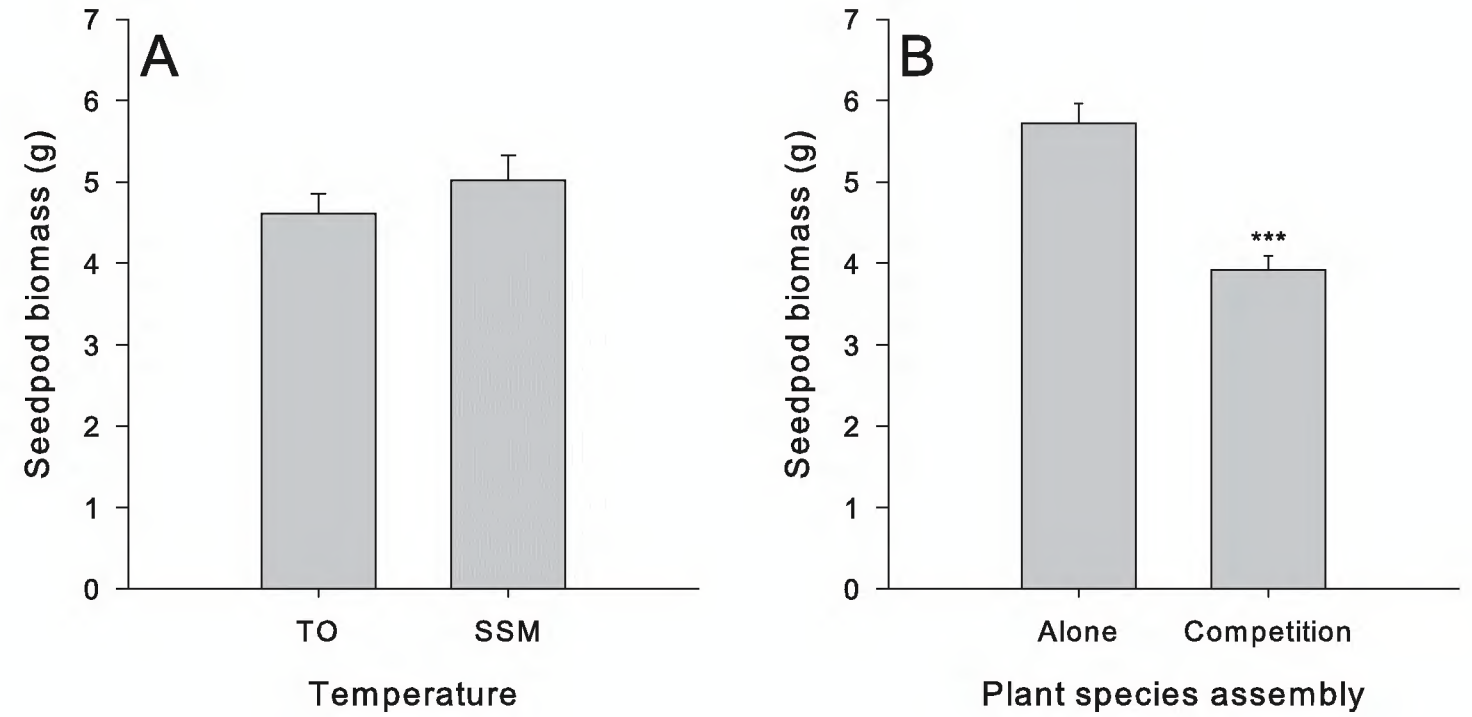

Figure 2. Effect of climatic temperature (i.e., Toronto (TO) and Sault Ste. Marie (SSM) and plant-plant competition (i.e., *V. rossicum* grown either alone or with *S. canadensis* (competition)) on seedpod biomass (A and B) and number (C and D) of *V. rossicum* at the end of the experiment. Significant differences between treatments are represented by *** ($p<0.00001$). Error bars represent the standard error of the mean (n = 24).

those grown in the warmer temperature ($F_{1,32}$ = 6.1587, p = 0.018). There was no significant temperature x competition interaction.

Root : shoot ratio of *V. rossicum* was 1.4-fold higher in plants competing with *S. canadensis* as opposed to those grown alone ($F_{1,35}$ = 9.3602, p = 0.004) (Table 2). This ratio was not affected by temperature (Table 2) or the combination of temperature and competition (data not shown). Conversely, the root : shoot ratio of *S. canadensis* was not affected by any factor or their interaction.

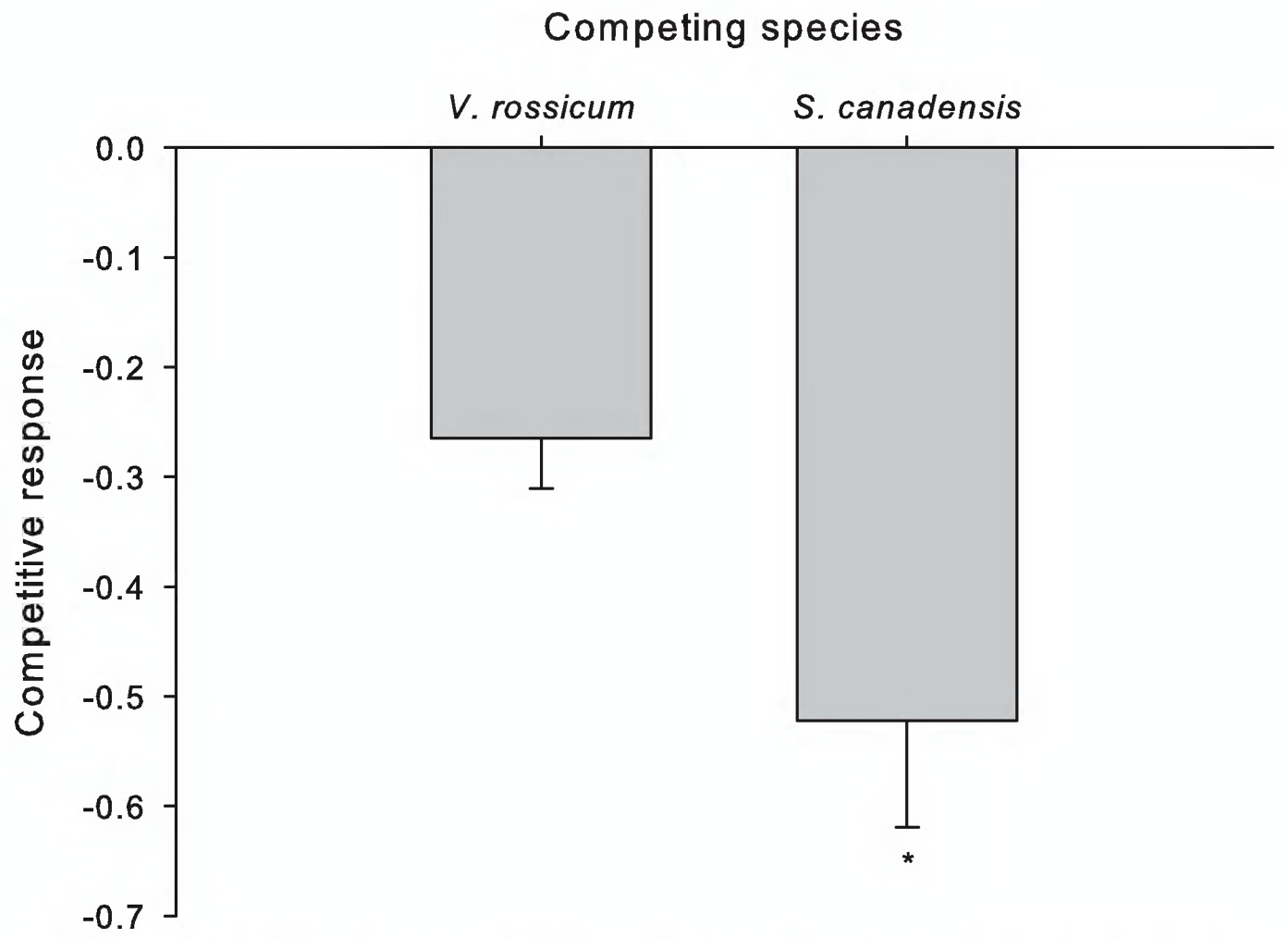

Figure 3. Competitive response (i.e., calculated by the ln of the relative yield, calculated by dividing the total biomass of an individual plant grown with a competitor by the average total biomass for that same plant species grown alone) of *V. rossicum* and *S. canadensis* relative to the presence of the competing species. Significant differences between species are indicated by an * ($p<0.05$). Error bars represent the standard error of the mean (n = 15 (*V. rossicum*; *S. canadensis*)).

Discussion

Temperature significantly affected the reproductive phenology of *V. rossicum*. Generally, phenological reproductive events took longer to occur under the cooler growing temperature conditions. This was expected as many plant species are known to accelerate their reproductive phenology when subjected to warming (Sherry et al. 2007), especially those with flowering times that occur before the peak of summer, as is the case of *V. rossicum*. Indeed, we found that a slight reduction from the current growing temperature conditions of *V. rossicum* was sufficient to produce a significant delay in budding, flowering, and the formation of seedpods. Along with photoperiod and moisture, temperature is considered a key environmental cue for flowering (Ratchke and Lacey 1985). Since we controlled for photoperiod and moisture, changes in the phenology of *V. rossicum* were likely solely influenced by temperature in our experiment. This is consistent with data indicating that some plants require the cumulative heatsum (i.e., a sum of daily heat inputs) to reach a certain threshold before flowering occurs (Reader 1983; Vasek and Sauer 1971; Ratchke and Lacey 1985). As such, we anticipate that *V. rossicum* will take longer to reach that threshold if it can indeed establish and overwinter in field soils from northern Ontario.

A plant's northern range is determined by its capacity to overwinter and then produce viable seeds (Morin et al. 2007; Chiune 2010). In this experiment the growing season temperature limit of *V. rossicum* was not reached, as all plants planted as root crowns produced mature seeds by the end of the growing season, which was simulated to coincide with the first frost in the SSM climatic region. This suggests that, despite experiencing a delay in reproductive phenology, *V. rossicum* can successfully produce as many propagules in the northern climate simulated in this experiment as in its current climate. Plants in their northern distribution ranges shorten their phenological timing to compensate for the shorter growing season, which can be done through phenotypic plasticity (Chuine 2010). It has been suggested that rapid seed maturation may be an adaptation to a later flowering time (Vasek and Sauer 1971). *Vincetoxicum rossicum* grown at lower temperatures produced mature seeds at the same time as those grown in warmer temperatures, suggesting an increase in seed maturation rate. As such, we conclude that phenotypic plasticity may enable this species to complete its life-cycle under the cooler climate of northern Ontario. However, our study focused on the growing season and *V. rossicum* started from root crowns. Future research should consider this species' potential to rapidly evolve, including its capacity to overwinter and grow under different (a)biotic conditions, upon establishment from seeds.

The native forb *S. canadensis* is highly abundant in disturbed areas in its native range and is an exotic invader in Europe and Asia (Abhilasha et al. 2008). The species is well adapted to cold climates; the center of the distribution range of *S. canadensis* var. *canadensis* is northern Ontario (USDA NRCS, National Plant Data Team). Indeed, we did find evidence for adaptation to the colder temperature conditions of our experiment as plants grown under the cooler SSM conditions were 1.5 fold larger than those grown in the warmer temperature. These features made it a suitable candidate to potentially reduce the spread of *V. rossicum* either intentionally through seed augmentation or naturally, particularly under northern Ontario temperature conditions. There has been some discussion as to whether some native species can be considered invasive within their native range and whether they should be treated differently than exotic invasive species (Davis et al. 2011). From that perspective, using a native species that is highly abundant in disturbed areas as a means of *V. rossicum* control could be problematic. However, various factors contribute to increase the risk of invasion by exotic relative to native species (see Simberloff et al. 2012) and considering that, overall, the most problematic biological invasions are caused by exotic species, we propose that investigating interactions between abundant native competitors and invasive exotic species should be considered both as a management option and in risk assessment.

We forced *V. rossicum* to compete against *S. canadensis*, which is highly abundant across the two climatic regions considered in this study. Competition between plants has been shown to reduce biomass, including allocation of biomass to reproduction (Weiner 1988). Indeed, seedpod biomass of *V. rossicum* plants grown in competition with *S. canadensis* was significantly smaller than that of plants grown alone regardless of growing season temperature conditions to which our variety of *S. canadensis* appeared to be adapted. Likewise, the total biomass of both *V. rossicum* and *S. canadensis* were

significantly reduced in response to competition. However, even though *S. canadensis* ultimately produced more total biomass than *V. rossicum,* it was more negatively influenced by competition. This may result in *V. rossicum* populations out-competing those of *S. canadensis* over time, even though we did not determine the fitness (i.e., seed production) response of *S. canadensis* to competition. Therefore, the method of seeding *S. canadensis* in areas invaded by *V. rossicum* as a control option to reduce its fitness and spread may be an inefficient approach in the long-term. Even more so if we consider that feedback with soil biota is likely to lead to greater pathogen accumulations and growth reductions in native compared to exotic plants (Klironomos 2002).

Several factors were likely to have contributed to the competitive advantage of *V. rossicum* relative to *S. canadensis* in relation to total plant biomass. Plants were not limited by water, light or space aboveground, which suggests that most competition would occur belowground for limited nutrient resources, which were supplied in low concentrations throughout the course of the experiment. *Vincetoxicum rossicum* increased its root : shoot ratio when in competition with *S. canadensis* whereas *S. canadensis* showed no response. This response of *V. rossicum* is consistent with competitively-driven adaptive plasticity, which can be explained by the balanced resource hypothesis; plants allocate nutrients and energy for growth to the areas responsible for the acquisition of limiting resources (Brouwer 1962). Competitively-driven adaptive plasticity has been shown in other plant species especially under limited nutrient regimes (Berendse and Möller 2009). The observed differential between the two species in their capacity to shift resource allocation towards roots when in competition suggests that this may be an important factor in the success of *V. rossicum* as an invader.

Goldberg (1990) proposed that if both competitors start as seedlings, the species that is better able to acquire resources has the competitive advantage. However, if one species has an initial size advantage, which was the case in our study (*S. canadensis* seedling competing with a *V. rossicum* plant started from a mature root crown), the species that is better able to tolerate resource limitation has a competitive advantage. Our data indicate that *V. rossicum* can both tolerate and scavenge for the limiting resources present. Although the size asymmetry may have led to some initial competition bias towards *V. rossicum*, our goal was to test whether *S. canadensis* could alleviate the invasion of already established *V. rossicum*. Nevertheless, future studies on competition between these two species could start equally from seeds. Future work should also investigate whether using a greater density of *S. canadensis* may be a more effective approach to help control *V. rossicum*. However, as discussed earlier competition and possible feedbacks with biota may favour *V. rossicum* in the long-term.

Vincetoxicum rossicum has been shown to be dependent on the association with arbuscular mycorrhizal (AM) fungi (Smith et al. 2008) and to be more heavily colonized by AM fungi in the field than other species grown in the same area (Greipsson and DiTommaso 2006). On the other hand, there is some evidence that *S. canadensis* may not be as mycorrhizal dependent as *V. rossicum* (Dhillion and Friese 1994). Indeed, in our experiment *V. rossicum* had lower root : shoot ratios than *S.*

canadensis, which is typical of more mycorrhizal plants (Oliver et al. 1983). The mesh utilized in our competition pots was designed to keep plant roots separate between species while allowing AM fungal hyphae to pass between the divided chambers. Therefore, we hypothesize that *V. rossicum*'s association with AM fungi may have facilitated access to the other half of the competition pot. Future work should focus on the role of soil biota as potential modulators of competitive interactions between native and exotic invasive species, which has not been consistently determined (Colautti et al. 2004; Levine et al. 2003).

Another possible reason for *S. canadensis* being a weaker competitor than *V. rossicum* could be that its timing for nutrient acquisition occurred later than that of *V. rossicum*'s. The two perennial species demonstrate different strategies; *V. rossicum* grows quickly early in the season whereas *S. canadensis* grows steadily over a longer period of time. A grassland study on invasion potential and resistance to invasion suggested that such resistance requires species that can establish and proliferate well, but also overlap the timing of their resource acquisition to that of the invading species (Young et al. 2008). It has also been suggested that the most accurate information about an invasive plant's competitive ability against native species comes from pairing the invasive plant with a functionally similar native species (Firn et al. 2010). Testing other competitor species that are more functionally similar to *V. rossicum* might provide further insight into the competitive ability of this invasive vine and its invasion potential when *S. canadensis* is not present.

Conclusion

In spite of a delay in reproductive phenology, the fitness of *V. rossicum* does not appear to be limited by cooler growing season temperature regimes found outside its immediate current distribution range in North America. Competition resulted in reductions in the fitness and total biomass of *V. rossicum* regardless of climatic temperature. However, the relative reductions in total biomass were greater for the competing native species *S. canadensis*.

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